

BEEVERIA (HOOKERIACEAE), A NEW GENUS FROM NEW ZEALAND

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INTRODUCTION

In the course of revising the New Zealand representatives of the Hookeriaceae *sensu* Brotherus for a moss flora of that country, it was concluded that the New Zealand endemic species currently known as *Pterygophyllum distichophylloides* Broth. & Dix. *in* Dix. constitutes an undescribed genus. Given the long-term nature of the New Zealand moss flora project and the recent high level of interest in the Hookeriales (*vide* Buck 1987; Tan and Robinson 1990; Crosby 1974; Allen and Crosby 1986), it is opportune to discuss this species here and to describe a new genus to accommodate it. A monotypic genus, named *Beeveria*, is described with notes on its relationships, synonymy, geographic distribution, and ecology.

BEEVERIA, GEN. NOV.

Pterygophyllum distichophylloides was described by Brotherus and Dixon (Dixon 1915) on the basis of a collection by Donald Petric from near Auckland. The species has received little subsequent taxonomic attention, probably due to its relative rarity. Treatments by Brotherus (1925) and Dixon (1927) have added little new information. Sainsbury (1955, p. 402) differentiated it from its congeners (in *Pterygophyllum*) by a combination of coloration, and leaf cell and margin characteristics. He also (p. 406) discussed the leaf areolation and the gemmae-bearing pseudopodia and used them as adjunct species characteristics. Sainsbury was the first, and seemingly the only, collector to find this species with capsules. He described the peristome in considerable detail, albeit with some internal inconsistencies (e.g., with respect to exostomial lamellae). While Sainsbury was impressed with the aggregation of peculiar features in *P. distichophylloides*, there is no suggestion that he considered it misplaced within *Pterygophyllum*.

Vitt and Crosby (1972) proposed *Achrophyllum*, a new generic name to replace the illegitimate *Pterygophyllum* Brid., and made appropriate combinations for two New Zealand species. They also stated the unelaborated opinion that *P. distichophylloides* should not be transferred to *Achrophyllum*. Neither Vitt nor Crosby has returned to the problem of the status of *P. distichophylloides*.

Numerous gametophytic and sporophytic features, including the presence of non-homologous vegetative reproductive structures, preclude the transfer of *Pterygophyllum distichophylloides* to *Achrophyllum* Vitt & Crosby (TABLE 1). There is no genus in the Hookeriaceae *sensu* Brotherus with the combination of gametophytic and sporophytic characteristics found in *P. distichophylloides* and thus a new genus is proposed.

Beeveria Fife, gen. nov.

Plantae vivae citrino-virides, siccae eiusdem coloris vel atrovirides. Caules prostrati, saepe in pseudopodia nuda, 2–3 mm longa, gemmarum capitulo terminata desinentes. Folia haud vel leniter asymmetrica, illa in seriebus dorsalibus ventralibusque ab illis in lateralibus vix divergentia, sicca valde crispata, elliptica, acuta vel apice infirme cuspidata, integra vel crenulata, limbo nullo. Costa singularis, simplex. Cellulae superiores laminales laeves, hexagono-isodiametricae, infirme vel modice collenchymatosae; cellulae marginales diversitatem nullam praebentes. Gemmae in capitulis terminalibus dispositae, anguste fusiformes, 160–240 μm longae, septis transversis 5–9 provisae. Dioeciae. Setae erectae, laeves. Capsulae 1.0–1.5 mm longae. Exostomatis dentes leniter sulcati, ca. 400 μm longi; endostoma membrana basali humili segmentisque perforatis praeditum. Sporae 10–15 μm , virides, subtiliter papillosae.

Beeveria distichophylloides (Broth. & Dix. in Dix.) Fife, comb. nov. FIG. 1

Pterygophyllum distichophylloides Broth. & Dix. in Dix., Bull. Torrey Bot. Club 42: 106, pl. 9, fig. 11. 1915. TYPE. NEW ZEALAND: near Auckland, 1892, *D. Petrie 800* (BM-Dixon!, WELT!).

Pterygophyllum colensoi Broth. ex Dix., Trans. New Zealand Inst. 3(5): 290. 1927, *nom. nud.* BASED ON: Sine loc., *Colenso 3115* (BM ex K).

The generic name honors Jessica E. Beever, whose collections and taxonomic work have greatly increased our knowledge of the New Zealand moss flora, especially that of the northern parts of the North Island, where *Beeveria distichophylloides* is most frequently collected.

Plants medium-sized, oily yellow-green when fresh, unchanged or dark-green when dry. Stems prostrate, sparsely to moderately branched, pale brown to yellow, to 4.5 cm, ca. 3 mm wide (including leaves), often ending in naked pseudopodia 2–3 mm long and terminated by a capitulum of gemmae; in cross-section with a distinct central strand, lacking a hyalodermis, with 2–4 cortical cell layers with moderately thickened walls; rhizoids on lower portion of stem dense, pale brown, \pm smooth, much-branched; pseudoparaphyllia foliose, lanceolate, ca. 300–400 μm long. Leaves inserted in 6 ranks, imbricate, complanate, nearly symmetric, those in dorsal and ventral ranks scarcely differentiated from those in lateral ranks, strongly crisped when dry, elliptic, tapered to acute or weakly cuspidate apices, plane, not concave, unbordered, entire (often somewhat crenulate due to collapsed walls of marginal cells in dry material), (1.0–)1.3–2.5(–2.8) \times 0.5–1.3 mm; costa single, ill-defined, ca. 35–60 μm wide at midleaf, markedly dilated in lowest third or more, unbranched, $\frac{1}{2}$ to more than $\frac{3}{4}$ the length of the leaf, in cross-section biconvex, lacking stereids; upper laminal cells smooth, thin-walled (ca. 2 μm at thinnest point), weakly to moderately thickened at corners, hexagonal-isodiametric, 24–42 μm diam., gradually becoming \pm oblong and non-collenchymatous toward base; marginal cells and alar cells not differentiated. Gemmae borne in terminal capitula, narrowly fusiform, 160–240 μm long, with 5–9 transverse septa. Dioicous; perigonia not seen (nor did Sainsbury, 1955, p. 406). Perichaetial leaves ovate-lanceolate, ecostate, ca. 1.2 mm long. Setae lateral, ca. (7–)9–11 mm long, erect, smooth, twisting weakly to the left throughout, red, ca. 150 μm diam., in cross-section lacking a hyalodermis, with 1–2 layers of thick-walled cortical cells and an ill-defined central strand; capsules pendent, ovoid from a short neck, 1.0–1.5 mm

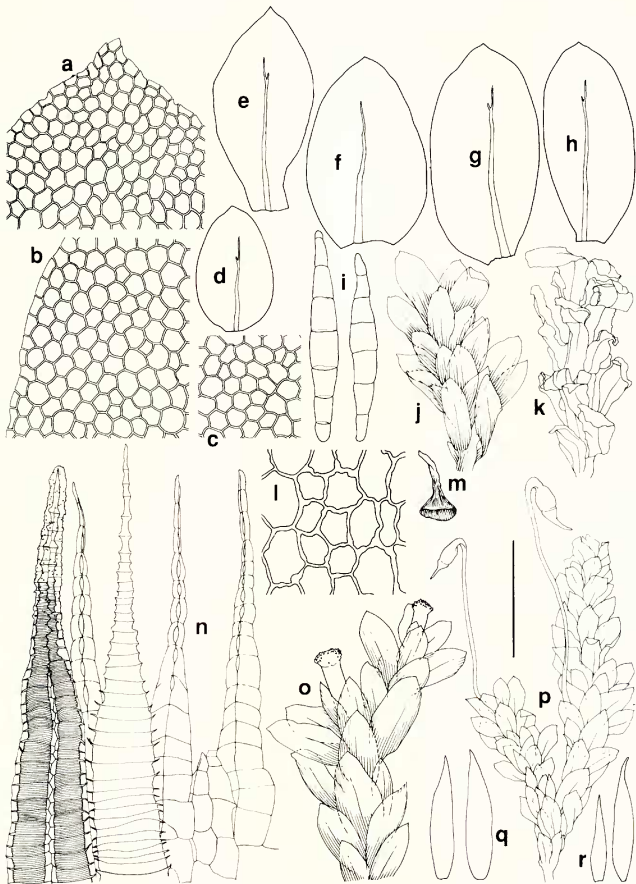


FIG. 1. *Beeveria distichophylloides*. a. Leaf apex. b. Margin at midleaf. c. Upper laminal cells. d-h. Leaf outlines. i. Gemmae. j. Moist stem. k. Dry stem. l. Exothecial cells. m. Operculum. n. Portion of peristome, showing outer and inner surfaces of exostome tooth, endostomial membrane and segments. o. Moist stem with pseudopodia. p. Moist stem with sporophytes. q, r. Perichaetial leaves. Scale = 165 μm for a-c, 1000 μm for d-h, q, r; 2300 μm for j, k, o; 100 μm for i, l, n; 3500 μm for p; 1400 μm for m. From Fife 6068 and Sainsbury 4388 (both CHR).

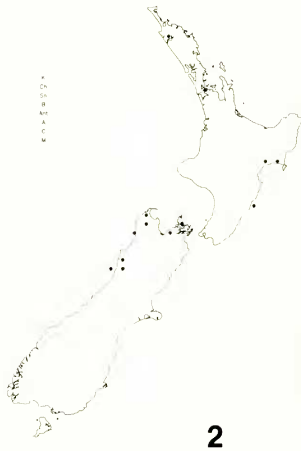


FIG. 2. Total distribution for *Beeveria distichophylloides*. Distribution dots centered on NZMS 260 1:50,000 topographic map sheets.

long, weakly constricted below the mouth and smooth when dry, reddish-brown; exothecial cells oblong to isodiametric, firm-walled, rather weakly thickened at corners, 12–18 μm in greatest diam.; annulus well developed, falling with the operculum; operculum long-rostrate from a conic base, ca. 0.8 mm long; exostome teeth yellow, lanceolate with a rather distinct shoulder, bordered, weakly furrowed (gap between portions of tooth less than 6 μm , extending to less than $\frac{3}{4}$ the length of the tooth, not visible with stereoscope), ca. 400 μm long, finely cross-striate below, baculate above, with adaxial lamellae projecting as weak trabeculae (6–9 μm long near base of tooth); endostome pale yellow, with basal membrane 100–120 μm high, segments ca. 260 μm long, nearly equaling the teeth, keeled and weakly perforate, papillose, cilia absent. Spores (10–)12–15 μm , green, very finely papillose. Calyptra mitrate, smooth, lobed at base [description from Sainsbury (1955, p. 405)].

Distribution. *Beeveria distichophylloides* is known only from New Zealand. There, it has a scattered distribution between latitudes 35° and ca. 42°19'S on the two main islands. It is recorded from North Auckland, Gisborne, Hawke's Bay, Nelson, and Westland land districts (FIG. 2). It is not known from any offshore island except D'Urville Island (Nelson Land District). It displays a distribution similar to that of nikau palm (*Rhopalostylis sapida*) and several mosses of northern affinities, e.g., *Braithwaitea sulcata*, *Catharomnion ciliatum*, *Ctenidium pubescens*, and *Tayloria callophylla*.

Ecology. *Beeveria distichophylloides* occurs on moist, shaded rock (usually, if not always, limestone) and clay or marl soil, often in association with stream margins or beds of intermittent watercourses. *Distichophyllum microcarpum* and *Achrophyllum dentatum* are frequent associates. It ranges in altitude from ca. 90–

TABLE 1. Comparison of character states in *Beeveria* and *Achrophyllum*.

Character	State in <i>Beeveria</i>	State in <i>Achrophyllum</i>
Dry coloration	Yellowish green	Brown or black
Shape of gemmae	Fusiform, transversely septate	L- or T-shaped, transversely septate
Location of gemmae	Terminal on pseudopodia	Epiphyllous on intramarginal cells
Nature of exostome tooth furrow	Less than 6 μm wide; not visible with stereoscope (40–50 \times)	Greater than 30 μm wide; visible with stereoscope
Length of exostome trabeculae	6–9 μm	18–24 μm
Height of endostomial basal membrane	ca. 100–200 μm	ca. 300 μm

300 m on the North Island and from 20–600 m in the northwest portion of the South Island.

Discussion. The generic name *Pterygophyllum* Brid. (Mant. Musc. 149. 1819) is illegitimate; a proposal to conserve this name against *Achrophyllum* Vitt & Crosby (Margadant *et al.* 1972) was rejected. A combination in *Achrophyllum* for *P. distichophylloides* has never been published. TABLE 1 summarizes the gametophytic and sporophytic features which distinguish *Beeveria* and *Achrophyllum*.

In *Beeveria*, gemmae occur in terminal capitula atop short pseudopodia and are fusiform and transversely septate. The pseudopodia of *Beeveria* are reminiscent of the unrelated genus *Aulacomnium*.

Sporophytically, the features that separate *Beeveria* from *Achrophyllum* are quantitative rather than qualitative (TABLE 1), but in aggregate they support generic segregation. In *Beeveria*, exostome teeth are weakly furrowed, short, and weakly trabeculate. The furrow is less than 6 μm wide at base, extends ca. $\frac{2}{3}$ the tooth length, and is not visible under stereoscope; the teeth are ca. 400 μm high, with lower trabeculae 6–9 μm long. In *Achrophyllum quadrifarium* (the genotype) the teeth are strongly furrowed, longer, and strongly trabeculate. The furrow is 30–36 μm wide at base, extends $\frac{3}{4}$ the length of the tooth, and is clearly visible under the stereoscope; the teeth are more than 700 μm high, with lower trabeculae 18–24 μm long. In *Beeveria*, endostomial segments are perforate and arise from a basal membrane ca. 100–120 μm high, while in the genotype of *Achrophyllum* segments are non-perforate and arise from a basal membrane ca. 300 μm high.

Buck (1987) synthesized the large amount of recent information and opinion (*vide* Tan and Robinson 1990; Crosby 1974; Allen and Crosby 1986) concerning the classification of the Hookeriales and proposed a reorganization of the order into five families. Buck's familial concepts place considerable emphasis upon gametophytic features and, despite some criticisms which have been leveled at them (*cf.* Tan and Robinson 1990), they are accepted here. Buck reduced the Hookeriaceae to only six genera (*Achrophyllum* Vitt & Crosby, *Cyathophorella* (Broth.) Fleisch., *Cyathophorum* P.-Beauv., *Dendroclyathophorum* Dix., *Hookeria* J. E. Sm., and *Schimpero-*

bryum Marg.); all other genera in Brotherus' Hookeriaceae are placed in four segregate families. He placed *Hookeria*, *Achrophyllum* and *Schimperobryum* in one "lineage" within his restricted Hookeriaceae. If Buck's evolutionary hypothesis is accepted, the lack of a central strand, the large, unbordered leaves, the short, hexagonal and porose leaf cells, the presence of pseudoparaphyllia, and other features in *Beeveria* dictate its inclusion in both the restricted family and in the lineage "centered around *Hookeria*." Within the "lineage" the nature of the leaf cells and the single, forked costae (interpreted here as synapomorphies) of *Achrophyllum* and *Beeveria* differentiate them collectively from *Hookeria* and *Schimperobryum*. By this interpretation, *Beeveria* and *Achrophyllum* are sister taxa, forming a clade whose relationship to *Hookeria* and *Schimperobryum* is not resolved.

The presence of pseudopodia and the fusiform, apical gemmae of *Beeveria* and the L- or T-shaped, intramarginal gemmae of *Achrophyllum* are apomorphies which differentiated the two allied genera. They suggest that *Beeveria* was not the ancestor of *Achrophyllum*, and the acceptance of *Beeveria* does not render *Achrophyllum* paraphyletic.

Differences in coloration of dried plants provide further distinction between *Beeveria* and *Achrophyllum*. The relatively weakly collenchymatous thickenings of the leaf cells, remarked upon by Sainsbury (1955, pp. 402, 406), are not considered significant as this feature varies markedly among various species of *Achrophyllum*.

Sainsbury's statements (1955, p. 406) that the exostome teeth of *Beeveria* (*sub Pterygophyllum*) *distichophylloides* lack both (adaxial) lamellae and median furrows, and that the median divisural line is more conspicuous relative to other species which he included in *Pterygophyllum*, are incorrect. Both adaxial (ventral) lamellae and a median furrow are present (but the latter is not visible under a stereoscope) and the "zig-zag" divisural line is no more conspicuous than in *Achrophyllum quadrifarium*.

No other genus in the Hookeriales bears gemmae in the manner of *Beeveria*. The one genus in the order with structures vaguely similar, the monotypic American-African genus *Adelothecium* (placed in a monotypic family by Buck [1987]), bears gemmae on axillary stalks on specialized microphyllous branches. The thick-walled, porose leaf cells, brownish pigmentation, lack of a central strand, and ascendent habit of *Adelothecium* are among many features which preclude the placement of *B. distichophylloides* in, or even close to, that genus.

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Howard Crum has provided guidance for many years and it is a pleasure to dedicate this contribution to him on the occasion of his 70th birthday.

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